

ASSEMBLAGES OF SPIDERS ON MODELS OF SEMI-ARID SHRUBS

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ABSTRACT. Many environmental factors influence the composition of animal assemblages. For spider assemblages, plant architecture is an important variable. Here we examine the effects of various plant architectural attributes by using models of shrubs in which we control branch orientation (horizontal or vertical) and height above the ground (0, 10, or 40 cm). Guild membership, based on hunting strategy (jumpers, pursuers, ambushers, or trappers), was used to characterize spider assemblages. Five replicates of the six treatments (two orientations by three heights) were randomly placed in a 60 m by 50 m grid among big sagebrush in a shrub-steppe habitat and sampled at 3 week intervals from July–October in 1997 and 1998. ANOVA was used to demonstrate that not only do single architectural variables influence the distribution of spiders but also the interaction of architectural variables influence spider distribution. Differences in the assemblages of spiders on the models were the result of architecture differences. Jumpers selected horizontal, 10 cm models and pursuers selected vertical, 0 cm models. Trappers were most abundant on horizontal, 0 cm models.

Keywords: Community ecology, plant architecture, shrub-steppe

The distributions of a wide variety of organisms are influenced by structural characteristics of their physical environment (MacArthur 1958; Wilson 1974; Rotenberry & Wiens 1980; James & Wame 1982; Landres & MacMahon 1983; Vander Wall & MacMahon 1984; Southwood 1996). In particular, plant attributes correlate with animal species diversity (Schoener 1968; Pianka 1973; Lawton 1986).

Spiders have been the focus of many community ecology studies because they are generalist carnivores, many species live in the same habitat and they are easily collected (Wise 1993). Several habitat structures correlate with spider abundance and diversity (Colebourn 1974; Gibson et al. 1992; Johnson 1995; Halley et al. 1996). Plant architecture was the specific subject of many studies (Fautin 1946; Chew 1961; Allred & Beck 1967; Allred 1969; Chaplin 1976; Gunnarsson 1988; 1990, 1996; Janetos 1986; Ward & Lubin 1992; Wise 1993; Sundberg & Gunnarsson

1994; Aiken & Coyle 2000; Ysnel & Canard 2000; Raizer & Amaral 2001).

The effect of plant architecture on the distribution of spiders on big sagebrush (*Artemisia tridentata*) has been the focus of several studies. Architectural features, such as herb height and shrub size were associated with the distribution of spiders (Abraham 1983). Changes in the density of individual big sagebrush altered the composition of the spider community (Hatley & MacMahon 1980; Wing 1984). Robinson (1981) and Ehmann (1994c) used models to simulate big sagebrush density, substrate diameter and horizontal and vertical orientation.

Guilds, based on mode of feeding (Root 1967), are widely used as dependent variables in studies of spider assemblages (Chew 1961; MacMahon 1973; Uetz 1977; Moran & Southwood 1982; Hurd & Eisenberg 1990; Pettersson 1996; Mason et al. 1997). Guild analysis provides a way to examine the organization of spider communities on big sagebrush (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984; Ehmann 1994a). Previous studies suggest that the guild composition of spider assemblages on big sagebrush is predictable despite differences in species

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composition (Abraham 1983; Ehmann 1994a). Although jumpers are ubiquitous and are found on the ground and on most vegetation, they dominate the spider assemblages found on big sagebrush. In the guild classification used by Ehmann, the spider community on big sagebrush was divided into four guilds (trappers, jumpers, ambushers and pursuers) using hunting strategy as a means of identifying guild membership. Trappers, including Araneidae, Dictynidae, Linyphiidae, Tetragnathidae and Theridiidae, construct webs to trap prey. Jumpers, Oxyopidae and Salticidae, actively seek prey using their well developed sense of sight to pounce on prey from a distance. Ambushers, Thomisidae, are sit-and-wait predators that wait for prey to move within striking distance. Pursuers, including Anyphaenidae, Clubionidae, Gnaphosidae, Lycosidae and Philodromidae, are active predators that run down prey.

In this study, the distribution of spiders by guild and a possible mechanism for the observed patterns were addressed using an experimental approach in the well-studied spider assemblage on big sagebrush. Two shrub characteristics stand out as making them architecturally different than the surrounding plants in shrub-steppe ecosystems. They are taller and they have more horizontal plant components. Shrub height has been associated with differences in spider community composition (Hatley & MacMahon 1980; Abraham 1983; Greenstone 1984; Döbel et al. 1990; Gibson et al. 1992; Lubin et al. 1993; Ward & Lubin 1993; Aiken & Coyle 2000; McReynolds 2000). Robinson (1981) used simple models to demonstrate that vertical/horizontal orientation affected the distribution of certain spider species. In this study, artificial shrubs were used to manipulate height and orientation of pseudobranches to determine the roles these two variables play in the distribution of spiders affiliated with specific guilds. Data from a four-year census of spiders on big sagebrush in the same area as the experiment were used to interpret results in relation to the natural system.

The specific purpose of this study was to measure the distribution of spiders affiliated with each of four guilds on models that simulated two plant architectural variables: height and branch orientation. Spider abundance on

each model served as the dependent variable in the analyses.

METHODS

Site.—This study was conducted at a 10 ha site 3.7 km east and 0.9 km north of the Hyde Park, Utah post office (NW1/4 SW1/4 sec 6, T 12 N, R 2 E, Salt Lake Meridian) at an elevation of 1755 m. The site was dominated by big sagebrush and grass with alfalfa fields on the east and west margins and steep canyons on the north and south. The experiment took place on the south side of a farm road that divided the site. This area has a southwest aspect and 5% slope. The part of the site north of the road was used for a four-year census. This site is 4 km north of the area used by Hatley and MacMahon (1980), Robinson (1981), Abraham (1983), and Wing (1984) and 7.5 km northwest of Ehmann's site (1994a).

4-year census.—An 80 m² grid was established and divided into quadrants to facilitate locating sampling points. The four corners, midpoints of each side and the center were permanently marked. In 1995, 20 shrubs were chosen for the census for each sampling day. After 1995 the number of shrubs sampled per day was increased to 24. Spiders were collected every 14–28 d from May until October in 1995–98. The number of sample days ranged from 7–13 totaling 42 for the four years. For each census day, five or six points within the grid were selected using a table of random numbers to identify the coordinates of the points. Sampling began 2 h after sunrise using the randomly selected coordinates. The four big sagebrush closest to the sampling point and meeting the established criterion (0.75–1.5 m high) were noted. The height criterion was established in order to sample similar sized big sagebrush because there is a positive relation between shrub size and spider abundance (Abraham 1983).

Spiders were collected from each shrub by using a beating sheet technique (Southwood 1978; Ehmann 1994a). Large spiders were captured by hand using vials and small spiders were captured with an aspirator. The beating sheet technique captures about 84% of the spiders on big sagebrush and the capture rate represents an unbiased sample of species found on the shrubs (Ehmann 1994b). Ehmann also showed that there was no effect on the sub-

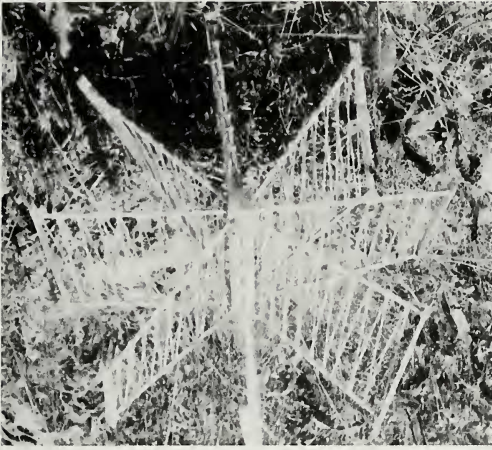


Figure 1.—Photograph of model in horizontal orientation.

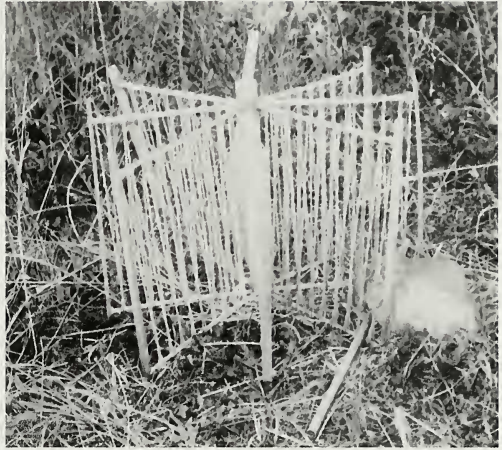


Figure 2.—Photograph of model in vertical orientation.

sequent sampling of the same shrub after a two-week interval. All spiders captured from a shrub were immediately placed in a vial with 70% ethanol for preservation. This process continued until the four shrubs around the first point were sampled. The second point was then located and the process repeated until all 24 shrubs were sampled.

Spiders were sorted by species and identified using the reference collection of Cache Valley spiders at Utah State University (Ehmann 1994b). Data were recorded as total species abundance and guild abundance per day. Guild assignments (jumpers, pursuers, ambushers, and trappers) followed the procedures used by Ehmann (1994a). Specimens were deposited in the Utah State University Entomology Collection. A pre-experiment census was also conducted, in the same manner, for one season (1997) in the area where the experimental models were placed.

The Jaccard index, a coefficient of similarity that gives an indication of the degree to which species composition overlaps between two locations (Southwood 1978), was used to compare assemblages of spiders in the experiment with the natural distribution found on big sagebrush.

Experiment with models.—The models for the experiment were constructed from wood and sisal twine and in some cases aluminum conduit (Figs. 1 & 2). A center post was the “trunk.” A “whorl” of eight dowels “branched” perpendicularly from each end. A wooden slat was used to keep the ends of the

branches 40 cm apart. Sisal twine wrapped around the dowels was used to represent smaller branches. The models were cylinders with 63 cm diameters, 40 cm heights and volumes of 124,690 cm³ (Heikkinen 2001). Shrub volumes measured in previous studies were 24,991–598,796 cm³ (Hatley & MacMahon 1980) and 120,000–311,000 cm³ (Wing 1984). Two orientations were tested (vertical and horizontal) by turning the model 90° on its longitudinal axis.

Three height positions were used for each of the vertical/horizontal orientations. One treatment was placed on the ground. In the second and third treatments aluminum conduit was used to raise the model 10 cm and 40 cm off the surface. The conduit was driven into the ground and then inserted in a hole drilled into the center post. Five replicates of each treatment were established on a 10 m by 10 m grid. Treatments were assigned to each point on the grid by random draw. Once a treatment was assigned to a point, it remained at that point for the year, but a second random assignment took place for the second year. Where sample points coincided with a shrub, the model was placed as close to the sample point as possible without touching a shrub.

Data were collected in 1997 and 1998 beginning in the last week of July and ending in mid-October. Spiders were collected from the models every 3 weeks using the beating sheet technique, and preserved in 70% ethanol. Specimens were sorted and identified in the laboratory and assigned to one of the four

guilds using the same procedures described above.

Data were analyzed using ANOVA (SAS 1982) where species the independent variable was an individual spider and the dependent variables were the spider's guild, the orientation of the model on which it was found, and the height of the model. All two-way and three-way interactions were tested.

RESULTS

Censuses of spiders on big sagebrush at Hyde Park.—A baseline for the interpretation of these experiments was established from censuses of spiders found on big sagebrush from 1995–1998 (Table 1). The jumper guild was most abundant each year containing 62.0% of the total individuals (range = 57.5–66.0%). Four jumpers were among the ten most abundant species across all guilds. *Pellegrina aeneola* Curtis 1892, a jumper, was most abundant accounting for 26.9% of the total. Other abundant jumpers were *Sassacus papenhoei* Peckham & Peckham 1895, *Oxyopes scalaris* Hentz 1894 and *Phidippus johnsoni* Peckham & Peckham 1883. The trapper guild was second most abundant with 21.1% of the individuals collected and it had three of the ten most abundant species: *Theridion petraem* L. Koch 1872, *T. neomexicanum* and *Metapeira foxi* Gertsch & Ivie 1936. Pursuers was the third most abundant guild with 12.9% of the total. The most abundant pursuers were *Philodromus histrio* Latreille 1819 and *Tibellus oblongus* Walckenaer 1802. Ambushers was the least abundant guild with only 2.9% of the spiders collected. One ambusher, *Xysticus gulosus* Keyserling 1880, was the tenth most abundant species.

Results of the experiment with models.—The Jaccard index yielded a similarity value of 0.55 between the Hyde Park census and the experiment. See Table 1 for a list of the species found in the census and the experiment.

Our principle hypothesis was that jumpers would be most abundant on shrub-like models, i.e., 40 cm models placed in a horizontal orientation. Since this was an experimental manipulation of two shrub variables which may effect the distribution patterns of all spider guilds, the significance of all variables (height, orientation and guild affiliation) and higher-order interactions were identified using ANOVA (Table 2).

Two variables were significant by themselves. Over half of all spiders collected were jumpers and about half of all spiders were on the 0 cm models (Table 3).

Although the assemblages of spiders based on guild membership from the censuses and the experiment were similar (Fig. 3), there were differences in the species composition of the assemblages. Jumpers was the most abundant guild in both cases (65.8% and 51.6%), however, *Pellegrina aeneola* was most abundant in the census, but accounted for only 1.4% of all spiders on the experimental models. Although pursuers were third most abundant in both treatments, they accounted for 11.0% of the spiders in the census, but 19.4% of the spiders collected from the experimental models. *Philodromus histrio* was the most abundant pursuer in the census (4.8%), but was only 0.2% of the spiders collected from the experimental models. *Tibellus oblongus* was more abundant on the experimental models: 17.9% vs. 4.2%.

The significant variables identified by the ANOVA only indicate that spiders are reacting differentially to architectural variables. Two-way interactions were examined to elucidate differences in spider distribution by guild based on differences in height or orientation. Even though orientation was not significant alone, height by orientation was also included because the complete model was analyzed. All two-way interactions were significant.

The guild by height interaction was significant because 86% of the pursuers and 44% of the trappers were on the 0 cm models. Orientation by itself was not a significant variable, about half were on models of each orientation; the interaction of orientation with guild and height was significant. Jumpers were more abundant on horizontal models (58%) and pursuers were more abundant on vertical models (81%). The height by orientation interaction was significant because 61% of the spiders on the 10 cm models were on horizontal ones and 57% of spiders on the 0 cm models were on vertical ones.

The three-way interaction was the analysis used to test our principle hypothesis that spiders belonging to specific guilds would be more likely to be found on specific models. For example, jumpers would be most abundant on tall, horizontal models. The three-way

Table 1.—Abundance of spider species found at Hyde Park and on the experimental models.

Species	Census				Experiment	
	1995	1996	1997	1998	1997	1998
<i>Sassacus papenhoei</i>	267	707	143	196	19	31
<i>Pelegrina aeneola</i>	251	966	433	717	4	2
<i>Phidippus johnsoni</i>	49	121	42	58	14	20
<i>Evarcha hoyi</i>	15	10	39	63	1	1
<i>Habronattus hirsutus</i>	13	15	1	0	0	0
<i>Tutelina similis</i>	2	12	4	19	2	4
<i>Pellenes hirsutus</i>	3	27	5	10	0	4
<i>Synagales idahoensis</i>	0	12	1	1	0	1
<i>Talavera</i> sp.	0	2	2	6	0	1
<i>Oxyopes scalaris</i>	221	628	81	306	44	85
Salticidae	0	10	4	0	0	2
Jumpers	821	2510	755	1376	74	147
<i>Philodromus histrio</i>	68	235	53	181	0	1
<i>Philodromus rufus</i>	0	24	5	4	1	0
<i>Philodromus</i> sp.	0	1	1	1	0	0
<i>Tibellus oblongus</i>	71	188	58	95	33	44
<i>Ebo evanses</i>	0	0	0	1	0	0
<i>Thanatus formicinus</i>	2	0	0	0	0	0
<i>Cheiracanthium inclusum</i>	5	74	23	23	2	2
<i>Anypaena pacifica</i>	1	3	1	0	0	0
<i>Zelotes subterraneus</i>	3	0	0	1	0	0
Gnaphosidae	5	1	1	2	0	0
Clubionidae	0	1	1	2	0	0
Unknown pursuer	0	1	1	0	0	0
Pursuers	155	528	144	310	36	47
<i>Xysticus gulosus</i>	21	116	12	28	5	7
<i>Xysticus cunctator</i>	0	2	0	0	0	0
<i>Xysticus montanensis</i>	2	1	0	0	0	0
<i>Xysticus</i> sp.	2	0	0	1	0	0
<i>Misumenops lepidus</i>	26	6	7	13	1	2
<i>Misumenoides</i> sp.	0	0	1	0	0	0
<i>Coriarchne utahensis</i>	6	2	2	4	0	1
Ambushers	57	127	22	46	6	10
<i>Theridion petraeum</i>	124	305	142	229	9	42
<i>Theridion neomexicanum</i>	36	61	104	57	11	1
<i>Theridion differens</i>	0	0	1	4	0	0
<i>Theridion</i> sp.	25	8	5	10	2	1
<i>Euryopsis scriptipes</i>	20	58	30	57	2	8
<i>Enoplognatha ovata</i>	0	3	1	3	0	1
<i>Diponea tibialis</i>	0	38	20	12	2	0
<i>Diponea nigra</i>	0	11	9	2	0	0
<i>Dictyna completa</i>	10	1	0	12	0	0
<i>Dictyna idahoana</i>	18	33	9	6	1	1
<i>Metepeira foxi</i>	27	85	50	73	12	11
<i>Erigone dentosa</i>	27	21	4	40	0	0
<i>Spirembolus mundus</i>	3	2	2	1	0	0
<i>Frontinella communis</i>	2	3	1	3	1	0
<i>Araneus gemma</i>	1	6	2	5	0	0
<i>Araneus displicatus</i>	1	4	1	4	0	1
<i>Aculepeira verae</i>	0	5	1	3	0	0
Aranidae	0	1	0	0	0	0
Linyphidae	0	0	0	3	0	0
Unknown trapper	0	4	6	3	2	1
Trappers	295	647	388	527	42	67
Unknown	93	4	3	1	0	0
Total	1421	3806	1312	2263	158	271

Table 2.—Results of the ANOVA of spider abundance on the experimental models.

Source	df	SS	MS	F	P
Replicates	4	1.210	0.303	0.45	0.7733
Guild	3	101.927	33.976	50.43	0.0001
Height	2	25.474	12.737	18.91	0.0001
Orientation	1	0.001	0.001	0.00	0.9666
Guild × Height	6	22.526	3.754	5.57	0.0001
Guild × Orientation	3	17.899	5.966	8.86	0.0001
Height × Orientation	2	4.617	2.308	3.43	0.0330
Guild × Height × Orientation	6	23.269	3.878	5.76	0.0001
Error	816	547.019	0.674		

interaction was significant, and jumpers were most abundant on the 10 cm horizontal models (Fig. 4). This meant that there were unique combinations of height and orientation which had greater abundances of spiders from particular guilds. The most obvious interaction was that 70% of all pursuers were on the 0 cm vertical models. Jumpers were about equally abundant on all model types, but the effect of the interaction is evident when the abundances for the 10 cm models are compared. Jumpers were most abundant on the 10 cm horizontal models and least abundant on the 10 cm vertical models. Twenty-nine percent of all trappers were on 0 cm horizontal models.

DISCUSSION

The spider community found on big sagebrush has a characteristic distribution of spider guilds that is dominated by jumpers (Ehmann 1994a; Abraham 1983). Previous studies suggested that plant architecture influenced guild abundance of spiders on big sagebrush (Ehmann 1994a; Wing 1984; Robinson

1981; Hatley & MacMahon 1980). In this study, the effects of two architectural variables on the distribution of spider guilds was tested using models that simulated the volume, branch texture and branch diameter of big sagebrush, while keeping the structural details simple enough to measure the two treatment variables (height above ground and branch orientation) and control for other variables. The models were placed among big sagebrush, so they were in the right habitat, and since spiders readily disperse (Dean & Sterling 1985; Bishop & Riechert 1990; Ehmann 1994b; Foelix 1996), they were in a habitat which contained a pool of potential colonists. Previous studies that examined habitat complexity, looked at the effect of single variables on the distribution of spiders. In this study, it was possible to test for the significance of the height by orientation interaction on the distribution of spider guilds. The significant three-way interaction indicated that branch orientation and height had a differential effect on guild abundance.

Table 3.—Total guild abundance for each model type over the two year (1997–1998) experiment using models to simulate shrub architecture. Numbers are the totals for seven sampling periods. Percentage of total abundance is in parentheses. 0 cm, 10 cm, and 40 cm = three height treatments. H = horizontal orientation and V = vertical.

Guild	0 cm		10 cm		40 cm		Guild totals
	H	V	H	V	H	V	
Jumper	44 (10.2)	41 (9.5)	54 (12.5)	22 (5.1)	31 (7.2)	29 (6.7)	221 (51.3)
Pursuer	13 (3.0)	58 (13.5)	1 (0.2)	7 (1.6)	2 (0.5)	2 (0.5)	83 (19.3)
Ambusher	2 (0.5)	5 (1.2)	3 (0.7)	2 (0.5)	5 (1.2)	1 (0.2)	18 (4.2)
Trapper	32 (7.4)	16 (3.7)	15 (3.5)	16 (3.7)	11 (2.6)	19 (4.4)	109 (25.3)
Model totals	91 (21.1)	120 (27.8)	73 (16.7)	47 (10.9)	49 (11.4)	51 (11.8)	
Height totals	211 (49.0)		120 (27.8)		100 (23.2)		

Guild Distribution

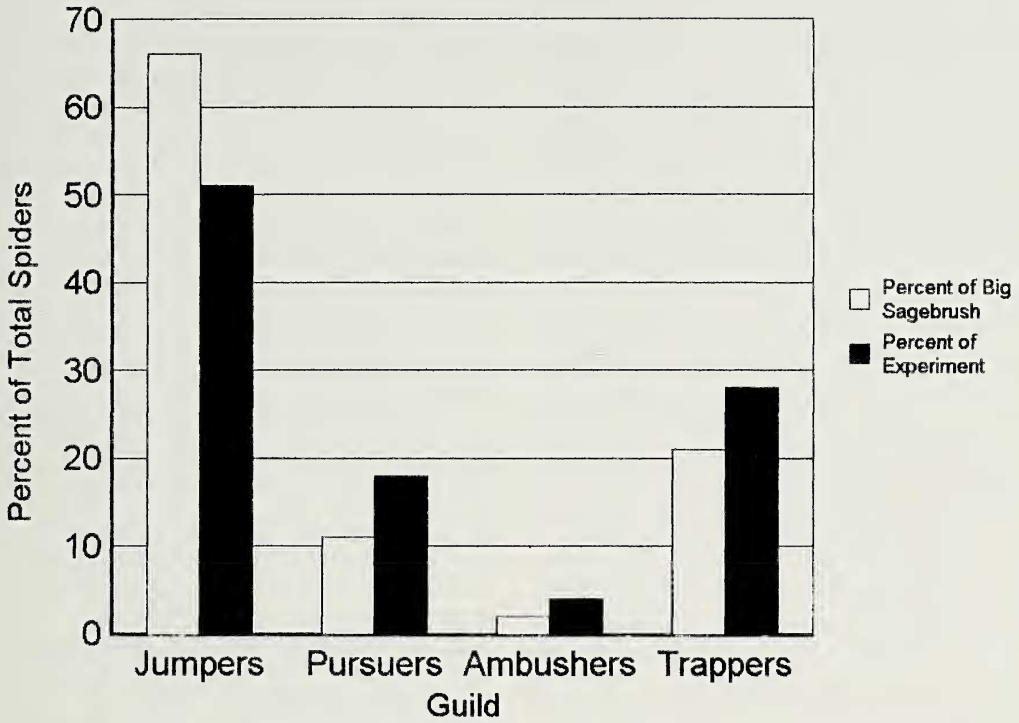


Figure 3.—Guild distribution of spiders from the Hyde Park census and from the experiment.

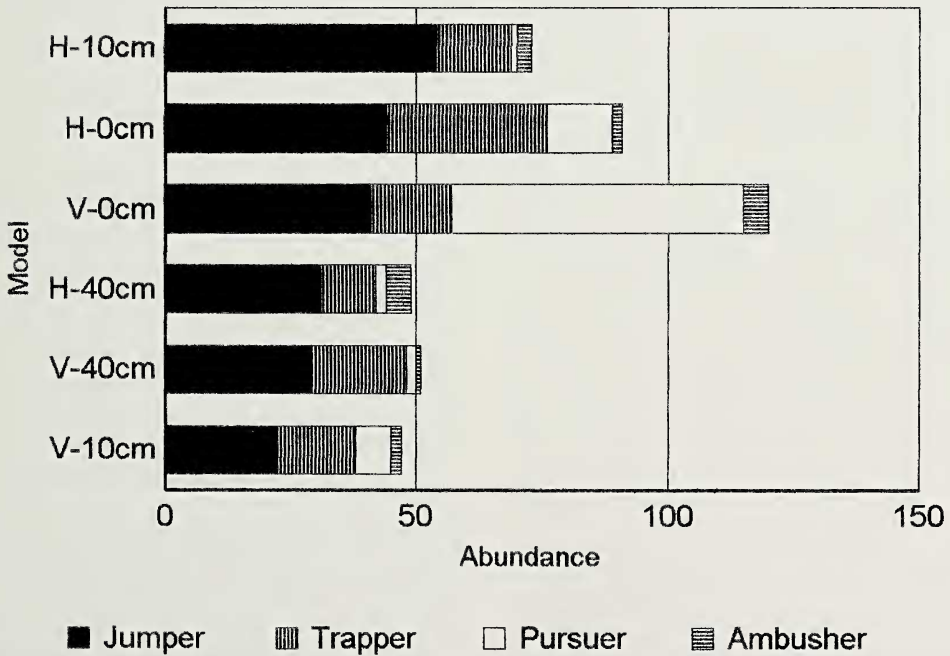


Figure 4.—Abundance of spiders by guild on models at two orientations (V = vertical and H = Horizontal) and three heights (0, 10, and 40 cm).

Seventy percent of all pursuers were found on the 0 cm, vertical models (Fig. 4). This model probably simulated grasses, and the most abundant pursuer in the experiment was *T. oblongus*, a grass specialist according to Roberts (1995), that is usually described as a sit-and-wait predator more like an ambusher than the other members of its guild (Gertsch 1979). The most common pursuer on big sagebrush at Hyde Park was *P. histrio*, but only one was collected from the models in the experiment.

Salticids and oxyopids are often more abundant on one vegetation type than another (Cutler et al. 1977; Abraham 1983). Jumpers are dominant on big sagebrush as they were on the horizontal models in the experiment. Jumpers were found in high numbers on all of the models, and there appears to be no differences between orientations on the 0 cm and 40 cm models. However, 71% of the jumpers on the 40 cm models were on those with horizontal orientations (Fig. 4). Sagebrush has significant horizontal components, so the horizontal nature of sagebrush may be one of the architectural variables to which jumpers are responding when they choose to remain on a shrub. The two-way interaction showed jumpers preferred horizontal models. In this experiment, jumpers were 51.4% of all spiders, which was within the range of jumpers found on big sagebrush in Hyde Park, but the most common jumper, *P. aeneola*, was virtually absent in the experiment. The decrease in numbers of *P. aeneola* was offset by higher numbers of *O. scalaris*. We do not know why there were species replacements. The important point is that there are redundant species and the guild distribution remained similar.

Salticids are among the most neurally sophisticated spiders (Forster 1982). The combination of a keen sense of sight, the ability to track prey even when the line-of-sight is interrupted and their unique jumping ability make them particularly adept at hunting in the structurally complex habitat found inside shrubs (Land 1969; Enders 1975; Jackson 1986; Jackson & Tarsitano 1993).

Jumpers may be using horizontality as a mechanism for recognizing that they are in a shrub, selecting habitat based on environmental cues (Orians & Wittenberg 1991). To understand these relationships additional studies are needed of the mechanisms responsible for

these responses (Rypstra et al. 1999) and the life history and foraging behavior of these species (Neuvonen 1999).

The three-way interaction for trappers demonstrates a more complicated height by orientation interaction. Forty-four percent of all trappers were on the 0 cm models. Of those, two-thirds were on the horizontal models. This result agrees with Robinson's (1981) finding. A interesting feature of this three-way interaction is that an opposite result was found for the models placed 40-cm above the ground. Twenty-eight percent of all trappers were on these models, but, in this case, 63% of them were on the vertical models.

The distribution of orb-web weaving trappers and cob-web weaving trappers (using Abraham's (1983) designations) also differed between these two treatments, with a higher proportion of orb-weavers on the taller vertical models and a higher proportion of cob-weavers on the horizontal ground models. Perhaps placing all spiders that use webs as snares in the same guild is too simplistic. Uetz et al. (1999) recently divided trappers into more than one guild.

Ambushers play a minor role on big sagebrush, as was true in the experiment. Ambushers are sit-and-wait predators. Many sit in the flowers of plants waiting to ambush pollinators. The small flowers of big sagebrush do not provide good sites from which to ambush prey. The majority of ambushers on big sagebrush are probably using crevices in the bark as retreats.

The significant three-way interaction demonstrates that spider decision-making involves a complex integration of environmental cues. The models were purposely simplified so the two variables of interest could be experimentally manipulated. The simplification had the effect of eliminating other variables, which are characteristic of big sagebrush, that spiders may also use as cues in the decision-making process. Some of these variables are bark texture, leaf structure, color, phytochemicals, and structural complexity. The result from this experiment that two of the most prominent members of the Hyde Park big sagebrush spider community, *P. aeneola* and *P. histrio*, were virtually absent on the experimental models in both years, indicates that the decision-making process probably involves more than two variables.

The experimental nature of this study made it possible to establish the cause and effect relationship among the architectural variables and the distribution of spider guilds. Spiders use architectural cues as part of the decision-making process to establish residency on shrubs or to make an attempt at colonization elsewhere.

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